Patterns and controls of ecosystem function in longleaf pine — wiregrass savannas. II. Nitrogen dynamics

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Abstract: The productivity of many temperate forests is nitrogen limited. Controls on N availability are particularly important in fire-maintained ecosystems such as longleaf pine – wiregrass (*Pinus palustris* Mill. – *Aristida stricta* Michx.) forests of the Coastal Plain of the southeastern United States, where periodic burning can result in substantial N losses. This study quantifies variation in net N mineralization across a complex ecological gradient for longleaf pine – wiregrass forests, from dry sandhills to wet–mesic sites adjacent to wetlands, for the first year after burning. Net N mineralization was consistently higher for the xeric site and declined as soil moisture status increased. Higher N availability was primarily due to higher rates of net nitrification in these plots, suggesting possible substrate-induced influences. Temperature was positively related to net N mineralization, while percent soil moisture was inversely correlated to net N mineralization. The greater N availability on dry sites may reflect greater quality organic matter inputs resulting from a significant hardwood (*Quercus laevis* Walt. predominately) component, and (or) it may reflect microclimate differences (warmer soil) that accelerate decomposition of detritus in soil.

Résumé : L’azote limite la productivité d’un grand nombre de forêts tempérées. Le contrôle de N disponible est particulièrement important dans les écosystèmes maintenus par le feu comme les forêts de pin des marais et d’aristide des pinèdes (*Pinus palustris* Mill. – *Aristida stricta* Michx.) de la plaine côtière du sud-est des États-Unis, où le brûlage périodique peut causer d’importantes pertes de N. Cette étude a permis de quantifier la variation de la minéralisation nette de N, le long d’un gradient écologique complexe, dans les forêts de pin des marais et d’aristide des pinèdes, depuis les collines de sable sec jusqu’aux sites humides–mésiques voisins des milieux humides, pour la première année qui suit le brûlage. La minéralisation nette de N est constamment plus élevée dans les sites secs et diminue à mesure que l’humidité du sol augmente. Une plus grande disponibilité de N est principalement due à un taux plus élevé de nitrification nette, suggérant une influence possible induite par le substrat. La température est reliée positivement à la minéralisation nette de N, alors que le pourcentage d’humidité du sol y est inversement corrélé. Une plus grande disponibilité de N sur les sites secs peut refléter un apport en matière organique de meilleure qualité résultant de la présence significative de feuillus (surtout de *Quercus laevis* Walt.) et (ou) refléter des différences microclimatiques (sol plus chaud) qui accélèrent la décomposition des débris dans le sol.

[Traduit par la rédaction]

Introduction

Longleaf pine – wiregrass (*Pinus palustris* Mill. – *Aristida stricta* Michx.) ecosystems dominated the Coastal Plain Region of the southeastern United States prior to European settlement (Ware et al. 1993). While a variety of anthropogenic disturbances have reduced the areal coverage of this ecosystem to approximately 2% of its original extent, a strong and growing interest in the management and restoration of longleaf pine – wiregrass forests has recently developed because of both ecological and economic rationales (Landers et al. 1995). Ecologically, longleaf pine – wiregrass forests are among the most floristically rich of temperate ecosystems (Walker and Peet 1983) and home to nearly two thirds of the threatened and endangered species (both flora and fauna) in the region (Noss 1989). Economically, these forests are valued for the high quality sawlog and pole products (Wahlenberg 1947), which have increased in stumpage rates dramatically over the past decade, and wildlife amenities, particularly bobwhite quail (*Colinus virginianus* (L.)) hunting (Rosene 1984). Understanding how structure and function of longleaf pine – wiregrass forests varies and is regulated is critical for the development of ecologically sound management regimes for these ecosystems (Christensen et al. 1996).

Longleaf pine – wiregrass ecosystems occur across a wide hydrologic gradient from xeric sandhills where scrub oaks, such as turkey oak (*Quercus laevis* Walt.), sand post oak (*Quercus margaretta* Ashe), and laurel oak (*Quercus hemispherica* Bartr.) are common associates, to the edge of

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wetlands, where slash pine (*Pinus elliottii* Engelm.) replaces longleaf pine as the dominant overstory species (Christensen 1988; Ware et al. 1993). Whereas the change in soil moisture availability across this gradient is conspicuous, the degree that other potentially limiting resources to productivity, such as nitrogen (N), vary across the gradient has not been quantified. Thus, predicting the availability of limiting resources (i.e., water and N), and, consequently, net primary production across these complex ecological gradients is currently not possible. This deficiency in understanding applies to many other forest ecosystems as well but is particularly acute for longleaf pine forests since research into the mechanisms regulating key ecosystem functions, such as N mineralization, across landscapes is still developing (Christensen 1981; Ware et al. 1993).

Soil moisture and N availability are generally thought to be positively correlated in forest ecosystems (Vitousek 1982; Pastor et al. 1984). The availability of soil resources may, in turn, influence future N cycling dynamics by regulating the quantity and quality of plant litter deposited to the detritus system. Mooney and Gulmon (1982) proposed a model that maintains that, as soil N availability increases, net photosynthesis also increases via higher photosynthetic rates per unit leaf area and (or) greater leaf area production. As a result, leaf tissues recover the cost of construction (i.e., achieve a net positive carbon balance) sooner on richer sites, and, thus, invest less in antiherbivore compounds such as lignin, astringent phenolics, and terpenes. This translates into shorter foliage retention times on richer sites (for evergreen conifers), which coupled with reduced nutrient retranslocation efficiencies, results in the deposition of more readily decomposable leaf litter. The more rapid decomposition and nutrient mineralization of these tissues with high N and low defense compound concentrations by the soil microbial community complete a positive feedback, which enhances soil N availability.

The quantity and chemistry of foliar litter may be particularly important in the N cycle of longleaf pine – wiregrass ecosystems since these forests are among the most fire dependent in North America (Olsen 1981), and litter quantity and chemistry affect fire behavior. Fire return intervals in the pre-European landscape ranged from 1 to 10 years with an average of approximately 2 or 3 years (Robins and Meyers 1992). Whereas microbial decomposition results in relatively gradual mineralization and tight conservation of N, burning promotes rapid N release and potential losses due to volatilization, particulate flux, and erosion (Christensen 1981; Raison et al. 1985). Thus, fire may result in increased N availability in short temporal scales but increases N losses at longer time frames (Ojima et al. 1994; Wright and Hart 1997). Feedback between resource availability and fuel quality, quantity, and spatial continuity have been proposed to affect oak composition in longleaf forests (i.e., greater oak density on xeric sandhill sites; Christensen 1987); however, no work has attempted to investigate the variation in ecological function such as N cycling.

The primary objective of this study was to assess the patterns and controls of N mineralization over a wide hydrologic gradient in longleaf pine – wiregrass forests during an annual cycle. Specifically we sought to (*i*) quantify patterns of N availability during an annual cycle after burning for three ecological site types (sensu Barnes et al. 1982; Pregitzer and Barnes 1982) characterized by differences in soil drainage classes and soil water holding capacity and (*ii*) relate patterns of N mineralization to differences in site microclimate, litterfall, and plant litter substrate quality. We hypothesized that (*i*) N mineralization rate would be positively correlated with soil moisture across complex gradients and (*ii*) increases in N mineralization and moisture availability would be associated with greater quantity and quality of foliar litter inputs and decreased N use efficiency across the gradient.

Methods

Site description

The longleaf pine – wiregrass ecosystems used in this study were located at Ichauway, a 115-km^2 reserve located in the Coastal Plain Region of southwestern Georgia. The climate for this region is characterized as humid subtropical (Christensen 1981), with an average annual precipitation of 131 cm that is evenly distributed throughout the year. Mean daily temperatures range from 21 to 34°C in summer and from 5 to 17°C in winter (Goebel et al. 1997). Ichauway is located within the Plains and Wiregrass Plains subsections of the Lower Coastal Plain and Flatwoods (LCPF) Province described by McNab and Avers (1994). The LCPF Province is a karst landscape, characterized by flat, weakly dissected alluvial deposits over Ocala Limestone (Arden et al. 1982). Parent materials are marine and continental sand and clay deposits formed during the Mesozoic (225–65 million years BP) and Cenozoic eras (65 million years BP to present) (Keys et al. 1995).

The longleaf pine – wiregrass ecosystems at Ichauway span the range of soil moisture conditions found in sites throughout the LCPF Province. We selected study sites with soils in three distinct drainage classes along this range: (*i*) excessively drained, (*ii*) moderately well drained, and (*iii*) poorly drained. The excessively drained sites (hereafter referred to as “xeric” sites) occur on upland sand ridges with undulating slopes of 3–4% and have deep, sandy soils, with no argillic horizon (i.e., no significant accumulation of clay) within 300 cm. The soils are Typic Quartzipsamments with a water-holding capacity in the upper 300 cm of approximately 18 cm water per metre of soil. The moderately well drained sites (hereafter referred to as “intermediate” sites) occur on upland terraces with undulating slopes of 2% and have loamy sands over sandy loams, with a depth to argillic horizon of approximately 150 cm. The soils are soils classified as Psammentic Kandiudults or Grossarenic Kandiudults with a water-holding capacity of 28 cm water per metre of soil. The poorly drained sites (hereafter referred to as “wet–mesic” sites) occur on upland terraces with nearly level slopes and have sandy loam over sandy clay loam or clay, with an argillic horizon present within 50 cm of the soil surface. The soils are classified as Aquic Arenic Kandiudults with a water-holding capacity of 40 cm water per metre of soil.

Ecological site classification: soils and vegetation

The xeric, intermediate, and wet–mesic study sites correspond to ecosystem types 13, 12, and 9, respectively, in a site classification system of Ichauway based on landscape position, soil type, and vegetation (Goebel et al. 1997). The vegetation of these sites has been maintained using understory prescribed burning with a return interval of 2–5 years, depending on fuel accumulation and moisture conditions. The xeric sites are dominated by open stands of longleaf pine, turkey oak, and scrubby post oak in the overstory, midstory, and understory, respectively. The intermediate sites are characterized by longleaf pine as a dominant overstory species, with blue-jack oak (*Quercus incana* Bartr.) and scrubby post oak

Table 1. Net N mineralization and nitrification for three longleaf pine – wiregrass ecosystem site types.

	Xeric ($kg\ N\cdot ha^{-1}\cdot year^{-1}$)	Intermediate ($kg\ N\cdot ha^{-1}\cdot year^{-1}$)	Wet–mesic ($kg\ N\cdot ha^{-1}\cdot year^{-1}$)
Net N mineralization LSD = 3.7	12.0 (1.1)*a*	7.8 (1.3)*b*	4.6 (0.6)*b*
Net nitrification LSD = 5.3	10.1 (1.4)*a*	4.3 (2.2)*b*	0.2 (0.1)*b*

Note: Values are mean annual rates of three plots per site type, with SE given in parentheses. Means within a row followed by the same letter are not significantly different at $\alpha = 0.05$.

occurring only as understory components. The wet–mesic sites are characterized by the single dominant, longleaf pine, in the overstory and midstory, with persimmon (*Diospyros virginiana* L.) occurring frequently in the understory. Dense ground cover at all sites is dominated by wiregrass with numerous species of other perennial grasses and forbs also present (Goebel et al. 1997).

Study design

Three study plots were established in each of the three ecological site types yielding a total of nine plots. Each plot was approximately 0.25 ha (50 × 50 m), although the xeric plots were increased slightly to include at least 55 longleaf pine trees. Ten subplots were located within each plot based on basal area. To locate the subplots, a 5 × 5 m grid was established in each plot and pine basal area (BAF 5) was measured at each intersection point of the grid. Pine basal areas were then divided into 20 percentile rankings, and two locations were randomly selected from each of the five percentile rankings yielding 10 subplots per plot.

Net N mineralization and soil moisture measurements

Nitrogen availability was estimated for a 12-month period (June to June) in each of the 10 subplots using in situ buried bag incubations of the mineral soil (Eno 1960). Ten soil cores (2-cm diameter) were collected from the 0–10 cm horizon in each subplot at the beginning of the incubation cycle, sieved at the laboratory, and subsampled for estimation of initial pools of inorganic N (NH_4^+ and NO_3^-) as well as soil moisture content. In addition, four subsamples were taken from each sample, placed in gas-permeable plastic bags, and buried (to 10 cm) in their original subplot within a 24-h period. After an incubation cycle ranging from 28 to 35 days, samples were retrieved, composited by subplot, and subsampled for inorganic N and soil moisture. Inorganic N in the initial and incubated soil samples was extracted with 2 M KCl (10 g : 25 mL) by vigorous agitation on a mechanical shaker for 15 min, followed by centrifugation for an additional 15 min. The supernatant for each sample was then carefully drawn off and frozen until NH_4^+ and NO_3^- concentrations were analyzed colorimetrically on a Lachat flow injection analyzer (Lachat Instruments, Inc., Milwaukee, Wis.). Ammonium N was analyzed by the indophenol-blue method, and nitrate N was reduced to nitrite using a Cd column and then determined by diazotiation (Keeney and Nelson 1982; Lachat Instruments Inc. 1992, 1997). Net ammonification and nitrification were then calculated by subtracting the initial concentrations from the final pools of extractable NH_4^+-N and NO_3^--N, respectively. Net mineralization was calculated as the sum of net ammonification and nitrification during the incubation period. All N flux estimates were calculated on a dry soil mass basis.

Gravimetric soil moisture values (g/g) represent the average between initial and final soil moisture for the incubation period. Patterns observed using gravimetric soil moisture measurements for the buried bag followed patterns using time domain reflectometry (v/v) soil moisture measurements when bulk density was accounted for (see Mitchell et al. 1999). Because of the lack of proper instrumentation, soil temperature measurements were not started until 4 months after the initiation of this study. Beginning in October 1995, temperature measurements to a 10-cm depth were taken biweekly using a single input digital temperature probe (Omega Engineering, Inc., Stamford, Conn.).

Litter analyses

Overstory litterfall was collected biweekly in 0.25-m^2 traps and separated into pine, oak, and "other" (e.g., branches, cones) categories. Dead wiregrass, which represented the dominant understory litter input across the landscape, was collected in late spring of 1996. Litterfall and wiregrass samples were dried at 70°C to a constant mass, weighed, and ground in a ball-mill grinder for subsequent chemical analyses. Samples were composited by litter type within a site for each sample period and analyzed for total carbon (C) and N on a Perkin Elmer CHN analyzer.

Statistical analyses

Mineralization data were analyzed using repeated measures (split plot in time) and a one-way analysis of variance (ANOVA) for individual sampling dates and cumulative totals. Mean levels of monthly and cumulative N fluxes, and litter quantity and quality measurements were compared using Fisher's protected least significant difference test with significance accepted at $\alpha = 0.05$ (SAS Institute Inc. 1990). Linear regression analyses were used to evaluate the influences of soil moisture and temperature on net mineralization patterns.

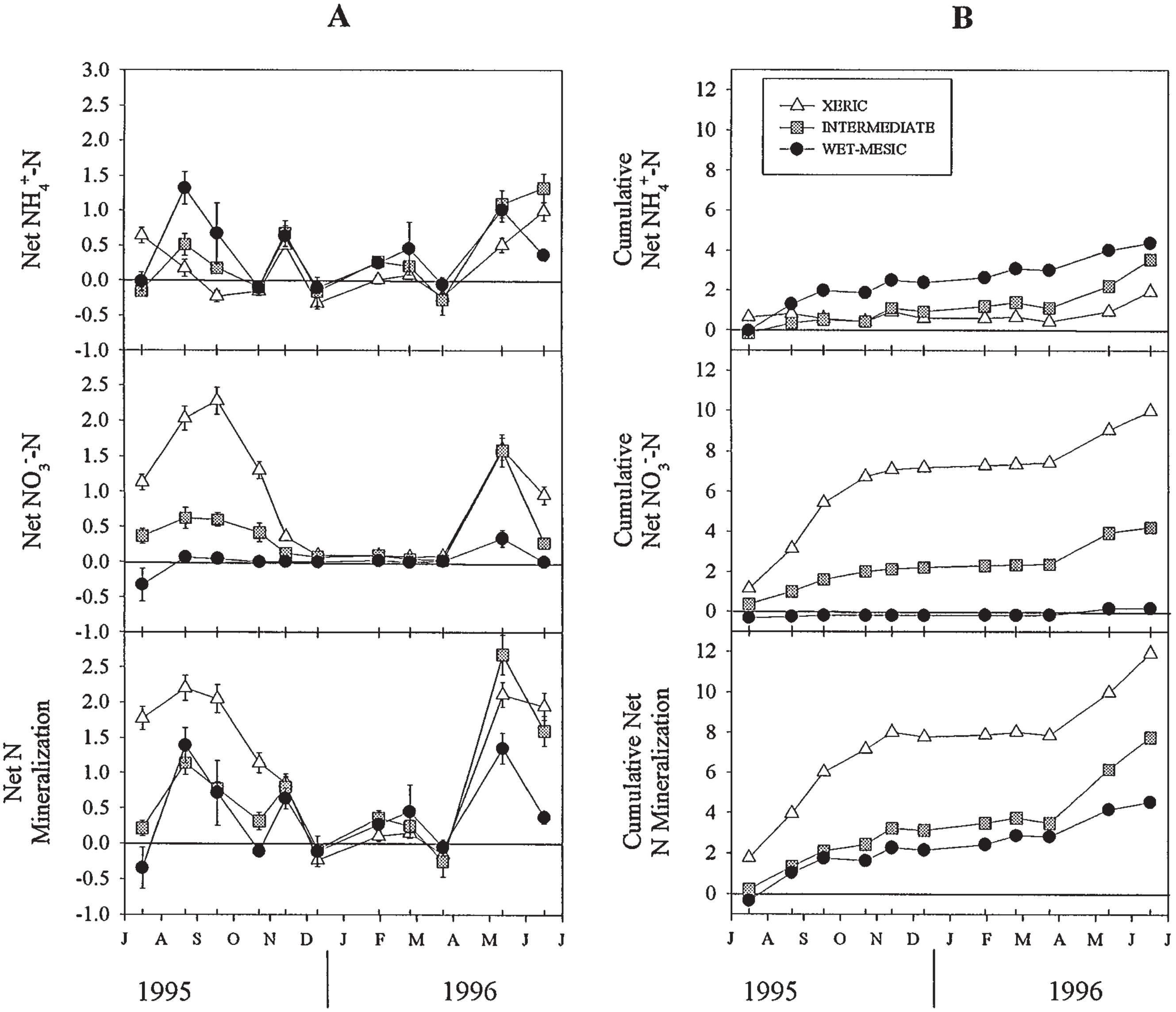
Results

Net nitrogen mineralization

Total net N mineralization rates were 4.6, 7.8, and 12.0 kg $N\cdot ha^{-1}\cdot year^{-1}$ for the wet–mesic, intermediate, and xeric sites, respectively (Table 1). Monthly rates of ammonification in the wet–mesic site were significantly ($P < 0.05$) higher than the xeric site during August and September 1995 and higher than the intermediate site in June 1996 (Fig. 1A). Otherwise, differences in monthly ammonification between sites were variable throughout the year and rarely significant. Cumulative rates of ammonification ranged from 1.93 to 4.38 kg $N\cdot ha^{-1}\cdot year^{-1}$ for the xeric and wet–mesic sites, respectively (Fig. 1B).

Net nitrification in the xeric site was significantly greater than the intermediate and wet–mesic sites during the summer of 1995 and higher than the wet–mesic site during the summer of 1996 (Fig. 1A). The cumulative rate of nitrification was significantly higher in the xeric site and was approximately 2.5 and 55 times higher than the rates measured in the intermediate and wet–mesic sites, respectively (Table 1). The relative rate of nitrification (i.e., nitrification

Fig. 1. Net rates of NH_4^+-N and NO_3^--N production and N mineralization (NH_4^+-N + NO_3^--N) in kg N/ha: (A) monthly rates (1SEM), (B) cumulative rates. Mean values calculated from 30 measurements per site.



divided by mineralization) was 4, 54, and 84% for the wet–mesic, intermediate, and xeric sites, respectively.

Temporal N-mineralization rates were significantly correlated ($P < 0.05$) with both temperature and moisture. These rates were positively correlated ($r^2 = 0.41$) with the soil temperature data (Fig. 2) but somewhat negatively correlated with soil moisture ($r^2 = 0.16$) (Fig. 3). Soil moisture on the wet–mesic site was consistently and significantly higher than the xeric site throughout most of the study with mean annual soil moisture values arrayed as follows: wet–mesic > intermediate > xeric (Fig. 4).

N transfers and litter quality

Longleaf pine litterfall dominated overstory inputs in the intermediate and wet–mesic sites (Table 2). In contrast, oak litter represented greater than 41% of litterfall in the xeric site (compared with less than 0.5% in the intermediate and wet–mesic sites). While overstory litterfall mass and N content were significantly lower in the xeric site, the N content of litter inputs was higher on this site because of the oak component (Table 2). Oak litter had an average C/N ratio of 57 compared with longleaf pine detritus, which ranged from 126 to 139 across sites. Other litter inputs (e.g., stems, bark, and seeds) were relatively minor and did not differ significantly between sites. Although dead wiregrass mass was significantly higher in the xeric site, the N contribution from this litter component did not vary significantly from the other two sites and the C/N ratio was intermediate.

Discussion

Net nitrogen mineralization patterns

The N mineralization rates measured across the ecological gradients in longleaf pine – wiregrass ecosystems in this study (range 4.6–12.0 kg N·ha^{-1}·year^{-1}) are among the lowest rates recorded for North American forests (Zak et al. 1989; Reich et al.1997). These rates are lower than those reported for other southern pine species growing on similar

Fig. 2. Relationship between net N mineralization and soil temperature at 10 cm depth across the gradient of sites. Mean values calculated from 30 measurements per site.

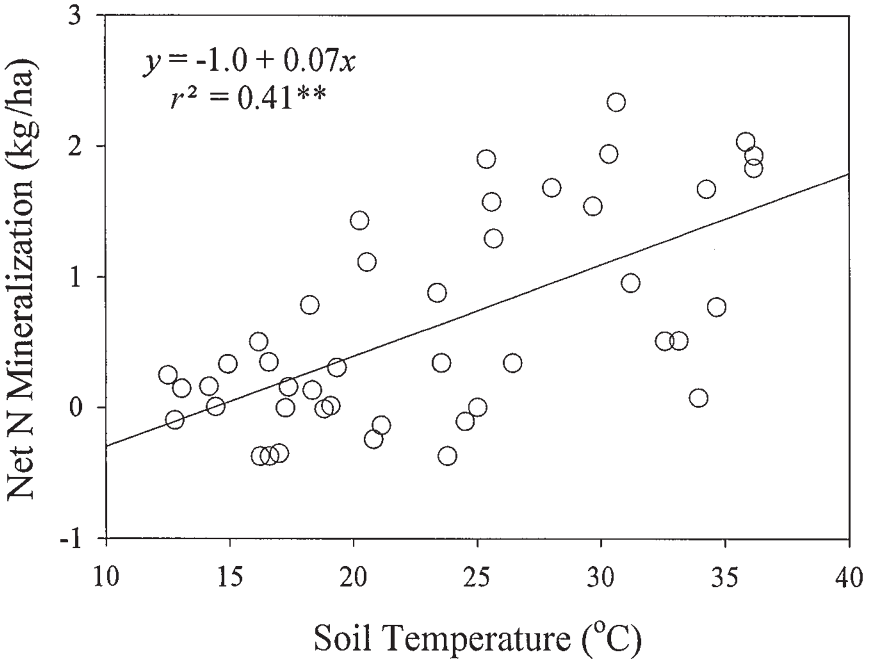
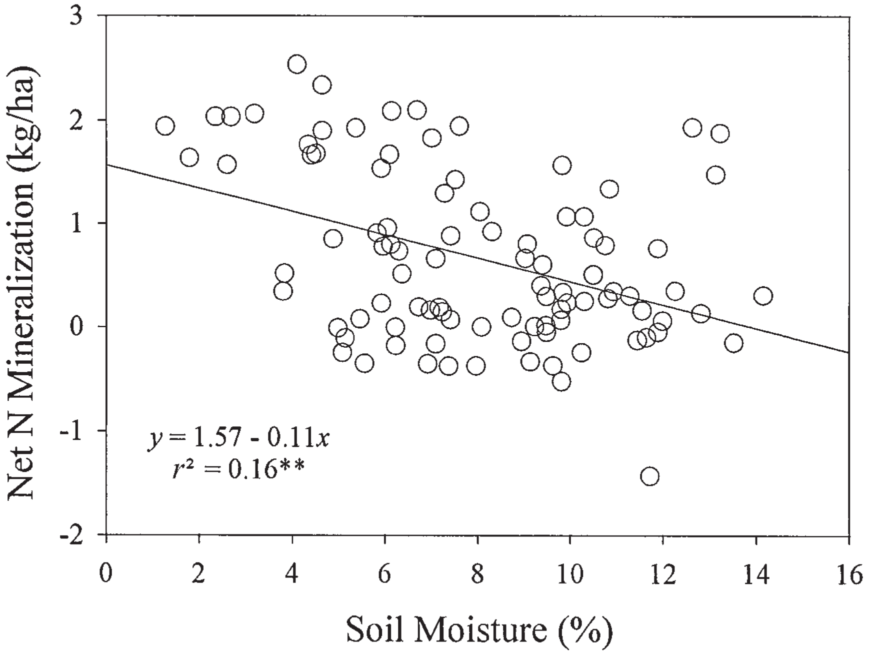
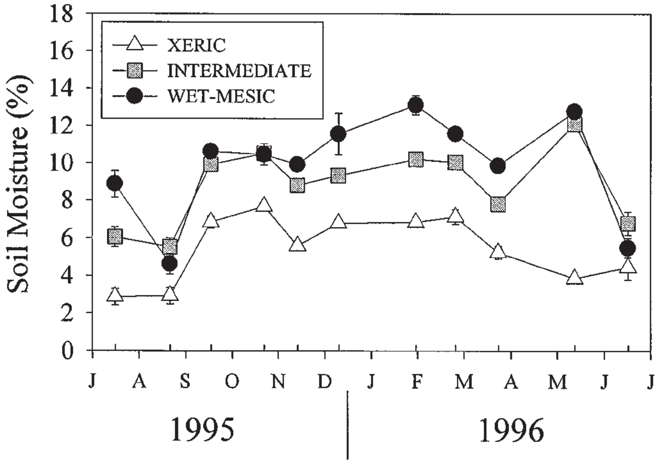


Fig. 3. Relationship between net N mineralization and soil moisture at 10 cm depth across the gradient of sites. Mean values calculated from 30 measurements per site.



site types (Gholz et al. 1985*a*, 1985*b*) and comparable with those measured in boreal coniferous forests, which have substantially shorter growing seasons and lower productivity rates (Cole and Rapp 1981). The low mineralization rates may be partially attributed to the effects of frequent burning, which create an “open” N cycle that is more characteristic of prairies than forests. Frequent fire (2- or 3-year fire return interval) eliminates or dramatically reduces the accumulation of a litter layer. Consequently, the surface soil organic matter content is not as highly enriched as compared with other forested ecosystems. However, fire may favor species in this ecosystem that could promote substantial N mineralization at depths greater than that measured in this study. Fire-adapted species such as those found in longleaf pine forests are perennials that typically allocate greater C and N reserves to belowground structures, resulting in relatively greater detritus inputs to soil from root turnover. The coarse texture of soil would allow for aeration, and the relatively

Fig. 4. Temporal patterns of soil moisture at 10 cm depth for the three sites. Mean values calculated from 30 measurements per site.



high temperatures may encourage N mineralization deeper in the soil profile.

Nitrogen mineralization was highest in the xeric ecosystem, which had the lowest measured aboveground net primary productivity (ANPP) across the gradient (see Mitchell et al. 1999) and progressively decreased as sites became more poorly drained. The inverse correlation between N mineralization and both soil moisture and aboveground production along this gradient is contradictory to our predictions, as well as other studies where N availability has been shown to increase ANPP. For example, N fertilization increased slash (Gholz et al. 1990) and loblolly pine (*Pinus taeda* L.) productivity (Albaugh et al. 1998) on sites similar to those used in this study. In addition, understory productivity was enhanced by fertilization across a moisture gradient in longleaf pine – wiregrass ecosystems in the Green Swamp of North Carolina (Walker and Peet 1983). The inverse relationship between N mineralization and ANPP observed here may indicate that, although both water and N may be limiting resources to productivity, water is more dominant than N in these ecosystems (Mitchell et al. 1999).

These results may also suggest that N is not the most limiting nutrient to productivity along part or all of the longleaf pine – wiregrass gradient used in this study. For instance, phosphorus (P) has been shown to limit productivity in some Coastal Plain forests in the southeastern United States (Pritchett and Smith 1975). However, extractable P was also inversely correlated with both moisture availability and aboveground production along the longleaf pine – wiregrass gradient (data not shown). This result is corroborated by the findings of recent studies indicating that potential N mineralization and extractable P vary in diametrically opposed ways to soil moisture along hydrologic gradients in longleaf pine – wiregrass communities (Jacqmain et al. 1998).

Microclimatic controls on nitrogen mineralization

The higher rates of N mineralization in the xeric site and the general increase in N mineralization during the summer suggests that temperature may be a dominant factor regulating N availability for these sites. Soil temperature accounted for 41% of the variation in N mineralization across all sites

Table 2. Mass, N content, NUE (nitrogen use efficiency), and C/N ratios for overstory and understory litter.

	Xeric				Intermediate				Wet–mesic			
Litter type	Litter mass (kg/ha)	N content (kg/ha)	NUE	C/N	Litter mass (kg/ha)	N content (kg/ha)	NUE	C/N	Litter mass (kg/ha)	N content (kg/ha)	NUE	C/N
Overstory												
Pinus palustris (foliage)	442 (126)*b*	1.83 (0.52)*b*	241*a*	126*b*	1998 (469)*a*	8.29 (1.94)*a*	241*a*	126*b*	2399 (388)*a*	8.98 (1.55)*a*	267*a*	139*a*
Quercus sp. (foliage)	446 (127)*a*	3.49 (0.95)*a*	128*a*	57*b*	8 (6)*b*	0.07 (0.05)*b*	114*ab*	57*b*	2 (1)*b*	0.02 (0.01)*b*	100*b*	67*a*
Other litter	194 (79)*a*	2.43 (1.19)*a*	80*b*	65*b*	208 (45)*a*	1.26 (0.31)*a*	165*a*	76*ab*	149 (37)*a*	0.83 (0.20)*a*	179*a*	85*a*
Understory												
Aristida stricta (dead)	476 (99)*a*	1.76 (0.37)*a*	270*b*	121*b*	345 (56)*a*	1.10 (0.18)*a*	314*a*	138*a*	353 (105)*a*	1.31 (0.39)*a*	269*b*	118*c*

Note: Values are means of three plots per site type. Values in parentheses for litter mass and N content are 1SE. Means of litter biomass, N content, NUE, or C/N in a row followed by the same letter are not significantly different at α = 0.05.

(Fig. 2) and was significantly higher in the xeric site when annual estimates were considered. The soil temperature differences among sites are not surprising considering that the xeric site is characterized by relatively patchy ground cover, which would allow for higher rates of direct solar radiation and, consequently, higher soil temperatures (Christensen 1987). The negative correlation between N mineralization and soil moisture along our gradient of sites, even though the relationship was weak (Fig. 3), was opposite in direction to that predicted. Soil microclimate has been widely demonstrated to affect microbial activity in laboratory and field studies, and our results support the general conclusion that temperature is the dominant factor controlling N mineralization processes (Nelson and Parkinson 1978; Schimel and Parton 1986; Burke et al. 1989; Kladivko and Keeney 1987; Schimel et al. 1997).

In addition to the direct stimulation of microbial and enzymatic activity, temperature may have influenced N availability indirectly via regulation of moisture availability in surface soils (Seadstedt and Knapp 1993; Blair 1997). Greater N mineralization rates were measured during the summer months (May to September) when soil temperature was generally higher and moisture was generally lower than the rest of the year. Fluctuations in soil moisture have been shown to affect N flux directly through the death of soil microbial populations and indirectly through the release and dissolution of occluded organic matter (Jager and Bruins 1975; Lund and Goksoyr 1980; Orchard and Cook 1983). Although the impact of alternating wetting and drying was not tested directly (i.e., microbial parameters were not measured), it is reasonable to assume that the cycles were probably more frequent and severe in the xeric site because of (*i*) low water holding capacity of the soil in xeric habitats, (*ii*) frequent light afternoon convection storm events that are characteristic of the summer months, and (*iii*) significantly higher soil temperatures observed for xeric sites.

The distinct differences in N availability among sites were attributed primarily to higher net nitrification rates in the xeric site, which raises the possibility that denitrification may have limited nitrate accumulation and, thus, N availability in the wetter sites. While denitrification was not measured in this study, most of the net N mineralization and nitrification occurred during the summer months when soils on all sites were the relatively driest of the year and the potential for denitrification assumed to be minor (Fig. 4).

Plant species controls on net nitrogen mineralization

In addition to microclimate, differences in soil organic matter pools may have influenced the N mineralization patterns across the complex ecological gradient. While foliar nutrient use efficiency (NUE; defined as litterfall mass/litterfall N) did not vary significantly among longleaf pines in different sites, NUE did vary between longleaf pine (241) and oaks (128) in the relatively N-rich xeric site (Table 2). Yin (1994) reported that NUE varied from 44 to 227 for deciduous stands and from 80 to 385 for evergreen forests, with evergreens having higher efficiency than deciduous species in areas of high light availability and temperature. Also, scrub oaks were in the lower range of NUE reported while longleaf pine was in the upper range. Satterson (1985) observed that white oak (*Quercus alba* L.) exhibited lower NUE than loblolly pine in a successional sequence in North Carolina.

As a result of lower NUE, oak leaf litter in the xeric site exhibited lower C/N ratios than either longleaf pine or wiregrass (Table 2). Numerous foliar decomposition studies have indicated that litter C/N is inversely correlated with mass loss and nutrient mineralization rates. This input of higher quality litter may have contributed to the higher mineralization rates in the xeric site. Klemendson (1991) reported that N mineralization rates in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forests were directly correlated to the percentage of Gambel oak (*Quercus gambelii* Nutt.) basal area. Wood et al. (1992) reported that soil supporting loblolly pine alone had significantly lower potential N mineralization rates than soil supporting diverse communities of pine, hardwoods, and herbaceous species. Moreover, Wedin and Tilman (1990) demonstrated the importance of particular plant species on N mineralization. They reported that, when different species of grasses were grown in soils that initially differed in N mineralization by nearly an order of magnitude, the rate of mineralization was more dependent on the species of grass than the soil type after only 3 years.

Although oak leaf litter quality was much greater than wiregrass or longleaf pine, aboveground litter in these systems is subjected to fire every 2 or 3 years, and much of the N contained therein is released to the atmosphere (Raison et al. 1985). Belowground litter inputs, however, are maintained in these systems and may provide substantial N capital to soil. Fine root turnover is important in regulating biogeochemical cycles in many forests (Zak and Pregitzer 1998); however, it may be even more critical in fire-maintained systems, such as longleaf pine, that typically have high carbon and nutrient allocation rates belowground. In frequently burned tallgrass prairies, Turner et al. (1997) have also hypothesized that N availability patterns could be driven, in part, by the quantity and quality of belowground inputs. Fine root decomposition studies using litterbags have indicated that mass loss rates are relatively slow compared with foliage and are inversely correlated with C/N and lignin/N ratios (Fogel and Hunt 1979; McClaugherty et al. 1985; Gholz et al. 1986; Grimm 1988). Although a generalized theory on foliage and N interactions (Mooney and Gulmon 1982) has been used as a framework to hypothesize N – fine root decomposition feedbacks, much less is known about root decomposition and its controls (Hendricks et al. 1993).

Finally, consistently higher net nitrification rates in the xeric site may also attest to the strong influences of soil organic matter quality on the N dynamics in these systems. In a laboratory incubation, Hart et al. (1994) observed increases in gross nitrification as labile C pools were exhausted, suggesting a shift in the microbial population from heterotrophs to predominantly autotrophic nitrifiers. In the xeric site, this shift may occur as labile C substrates are exhausted and autotrophic nitrifiers become more competitive for available NH_4^+ pools. The extent that C limitations may be influencing the microbial community in the xeric site and, in turn, the rate of nitrification needs further study. Future work relating gross mineralization rates and N availability patterns may illuminate these mechanisms more clearly.

Conclusions

We have shown that, contrary to our predictions, net N mineralization rates were negatively correlated with site moisture status. The decrease in net N mineralization as site soil moisture status increases appears to be due to influences of both microclimate and organic matter. Temperature was positively correlated to N mineralization, while simple correlation showed a weak negative correlation of N mineralization and gravimetric soil water content. Reciprocal incubations (xeric site soils incubated on both xeric and wet–mesic sites, and wet–mesic soils incubated at xeric and wet–mesic sites) may shed more light in the relative controls of microclimate and organic matter quality of soil detritus. The high rates of nitrification on the xeric site may point to interactions between litter quality of soil organic matter and microbial dynamics. Gross mineralization studies coupled with soil CO_2 flux may be useful in further investigations. The low rates of net N mineralization in the top 10 cm of soil may not be a reliable index of N availability in these systems, as a greater proportion of N mineralization may occur at lower soil depths relative to other forested ecosystems.

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